

ON THE STRUCTURE OF LEAVES OF *RHABDOTAENIA* PANT FROM THE RANIGANJ COALFIELD, INDIA

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ABSTRACT. A new species of *Rhabdotaenia* Pant (*R. fibrosa*) and additional details of epidermal structure of *Rhabdotaenia danaeoides* (Royle) Pant, based on a number of leaf fragments, collected from the Raniganj coalfield, India, are described. It is pointed out that these two species and *R. harkinii* Pant, are all structurally distinct.

TONGUE-SHAPED leaves found in the *Glossopteris* flora include, besides *Glossopteris* and *Gangamopteris*, the three other forms, *Noeggerathiopsis*, *Palaeovittaria*, and *Taeniopteris*. Pant (1958) has assigned some of these *Taeniopteris* leaves to a new genus *Rhabdotaenia*, in which he distinguishes two species, *R. danaeoides*, based on three incomplete leaves from the Raniganj coalfield, India, and *R. harkinii*, based on a single leaf fragment from East Africa. A third species, *R. fibrosa*, which shows interstitial fibres, is described here from the Raniganj coalfield. Besides these, additional characters of *R. danaeoides* are also described from numerous compressions of leaves of the species from the same locality.

Genus *RHABDOTAENIA* Pant

Rhabdotaenia fibrosa sp. nov.

Plate 49, figs. 1-7; text-figs. 1, 2B-E

Diagnosis. Leaf large, elongated oval, length unknown, 3.5-9.5 cm. wide, lamina widest in middle region, tapering towards apex. Apex acute, margins entire, midrib up to 3 mm. wide in middle region, narrower towards apex, showing many longitudinal strands towards base, fewer above. Lateral veins parallel, arising at an acute angle from midrib and almost immediately arching outwards and running at about 90° to midrib. Vein ends near margin sometimes slightly curved towards apex, but marginal veins or loops not seen. About one-fifth of total number of lateral veins forked once, forking either at point of origin from midrib or elsewhere in lamina. Forked veins less frequent towards apex. Concentration of veins 15-27 per cm. near midrib and 19-31 per cm. towards margin. Veins normally up to 167 μ thick. Areas between lateral veins often showing interstitial fibres, fibres up to 45 μ thick.

Upper epidermis of lamina nonstomatiferous. Cells between veins sinuous-walled, amplitude of sinuosities of cell walls averaging at 5 μ , average lateral distance between two antinodes 9 μ . Cells rectangular, arranged in longitudinal rows parallel to veins, typically averaging at 93 μ long \times 36 μ wide. Average thickness of walls 5 μ in middle region and 8 μ near midrib. Cells over veins narrower and longer with less sinuous sides. Surface of cells vaguely mottled, papillae not seen.

Lower epidermis of lamina stomatiferous. Cells between veins usually averaging at 79 μ long \times 60 μ wide, cell walls slightly more sinuous than in upper, amplitude of

sinuities of cell walls $7\ \mu$, lateral distance between two antinodes $15\ \mu$. Cells less regularly arranged than those of upper epidermis and elongated in various directions. Cells over veins narrower, elongated in direction of veins, sides of cells over veins less sinuous. Surface of cells clearly mottled, occasionally showing median hollow papillae. Trichomes absent. Stomata haplocheilic, unevenly distributed in areas between veins and normally absent in vein courses. Guard cells irregularly orientated, exposed, generally $51\ \mu$ long \times $19\ \mu$ wide, stomatal opening $6\ \mu$ wide. Subsidiary cells 3–5, irregularly shaped like ordinary epidermal cells; polar subsidiary cells unspecialized and like laterals.

Upper and lower epidermis of midrib showing rectangular or polygonal cells tending to be arranged in longitudinal rows; cell rows forming bands of narrow almost straight-walled cells (above longitudinal strands of midrib), alternating with bands of somewhat wider slightly sinuous-walled cells (in areas between midrib strands). Surface of epidermal cells above and near midrib often showing longitudinal surface striations.

Upper and lower cuticles of lamina like respective epidermal layers, surface mottled, cell outlines usually well defined over veins but often obscure between them.

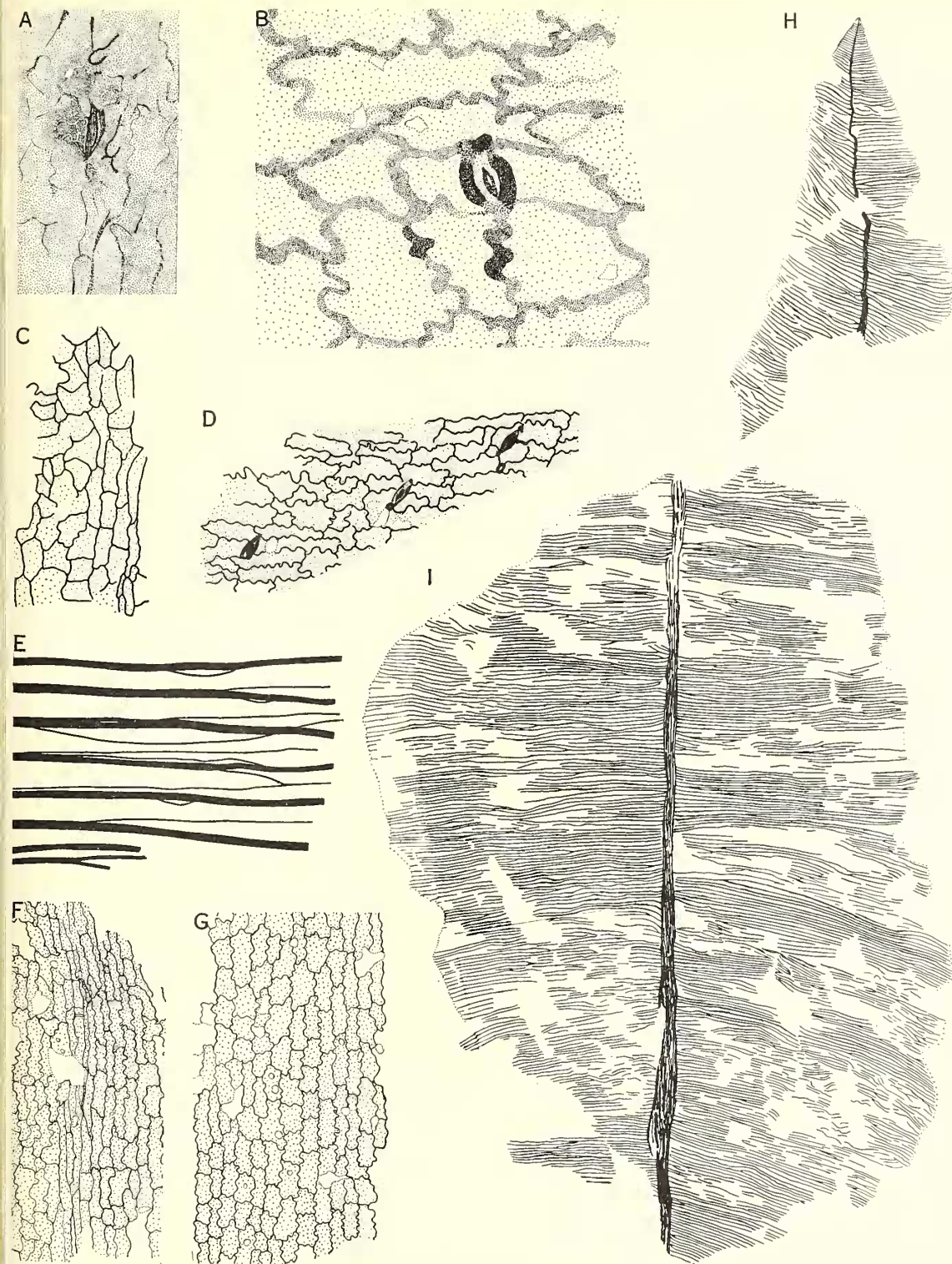
Holotype. Specimen No. 229 of Divya Darshan Pant Collection at present located in Botany Department, University of Allahabad, Allahabad, India.

Locality and horizon. Raniganj coalfield, India. Lower Gondwana.

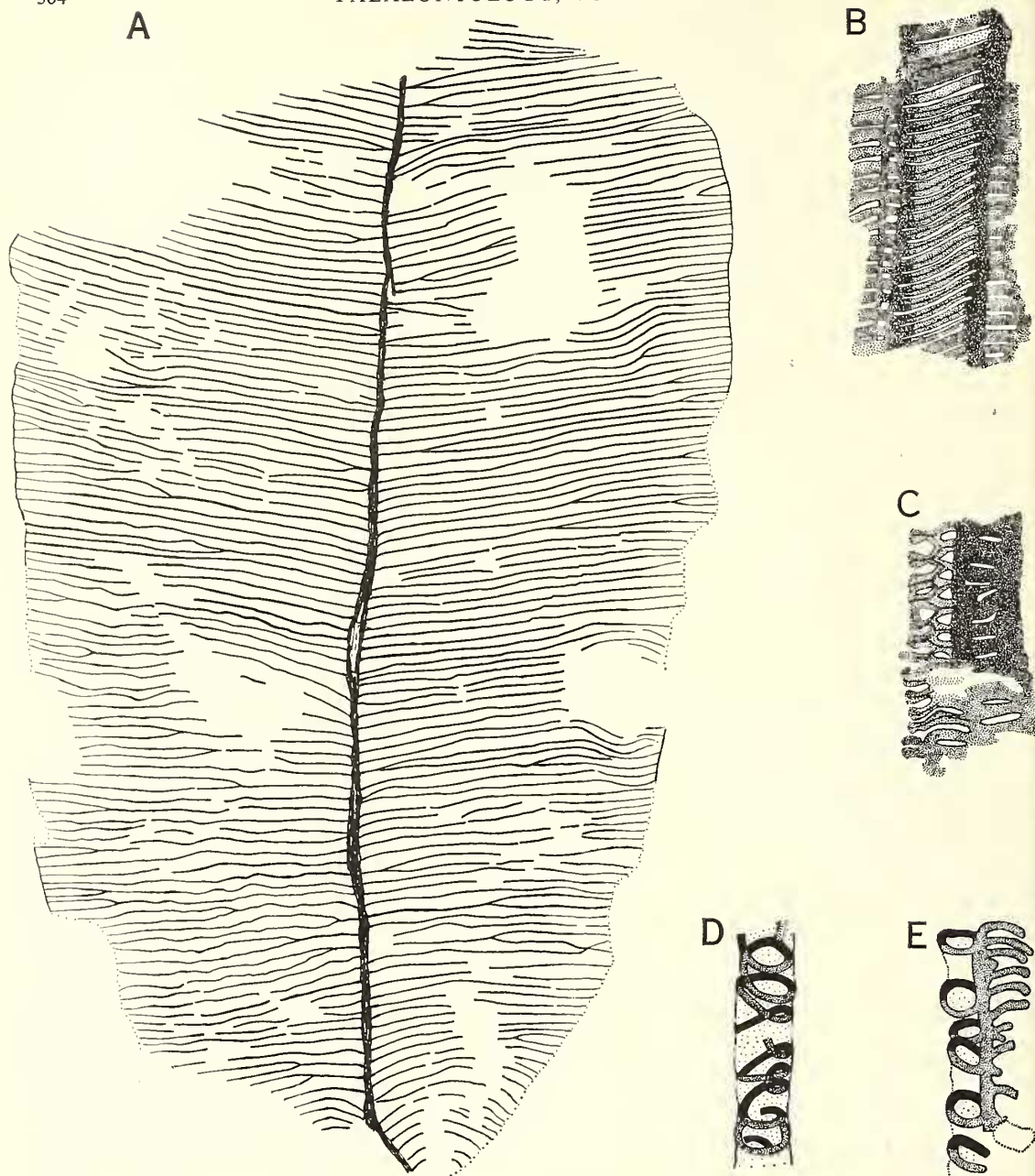
Description. The species is based on nine fragments of leaves, including one apex and eight pieces representing middle portions. None of our specimens shows the basal part of the leaves. The single apex is acute but its concentration of veins and epidermal structure are like those found in other fragments assigned to this species although interstitial fibres are seen only at a few places in the apical fragment. The width of various fragments from middle region of leaves varies from 3.5 to 9.5 cm. Lateral veins, which run almost straight up to the margin, are 62 – $167\ \mu$ thick. Displaced lateral veins, like those of *R. danaeoides* and *R. harkinii*, sometimes appear sinuous (Pl. 49, figs. 1, 7; text-fig. 1H, I). In an incident-light examination, small compressed creases and folds in the lamina may sometimes appear like anastomoses between lateral veins, but such apparent anastomoses can be clearly made out in transmitted-light examination of celloidin pulls, as the cells above vein courses run straight without anastomoses. Actual connexions between veins were never seen.

Interstitial fibres, which are 22 – $45\ \mu$ thick, come out of the lateral veins, usually in the middle part of the lamina. For some distance the fibres run between two veins and

TEXT-FIG. 1. *Rhabdotaenia fibrosa* sp. nov. A, Lower cuticle of lamina showing obscure epidermal cell outlines. 231d; $\times 267$. B, Lower epidermis of lamina showing an enlarged stoma with lignified lateral and polar lamellae (the lamella at the lower pole is broken (see also Pl. 49, fig. 3). 232a; $\times 267$. C, Lower epidermis of midrib showing elongated cells above vein and longitudinal rows of slightly sinuous-walled rectangular cells between them. 232a; $\times 83$. D, Lower epidermis of lamina with irregularly arranged sinuous-walled cells and stomata. 232a; $\times 83$. E, Side veins of lamina (thicker lines) showing interstitial fibres (thinner lines) between them (see also Pl. 49, fig. 4). 232; $\times 10$. F, Upper epidermis of lamina showing longitudinal rows of almost straight-walled narrow cells above a vein and wider cells with more sinuous sides on its two flanks. 232b; $\times 83$. G, Broader upper epidermal cells in area between two veins. 229; $\times 83$. H, Apical portion of lamina showing venation (see also Pl. 49, fig. 1). 233; $\times 1$. I, Middle portion of lamina showing furcate or simple parallel lateral veins diverging at a wide angle from longitudinally striped midrib (see also Pl. 49, fig. 7). 229; $\times 1$.



TEXT-FIG. 1



TEXT-FIG. 2. A, *Rhabdotaenia danaeoides*, B-E, *Rhabdotaenia fibrosa* sp. nov. A, Middle portion of lamina showing venation (see also Pl. 50, fig. 1). 251; $\times 3/2$. B, Xylem element from midrib showing scalariform thickenings. 231a; $\times 800$. C, Xylem element from midrib showing alternate biseriate pits (see also Pl. 49, fig. 5). 231a; $\times 800$. D, Xylem element from midrib showing spiral thickenings (see also Pl. 49, fig. 6). 231a; $\times 800$. E, Xylem element from a vein showing annular thickenings (see also Pl. 49, fig. 2). 234; $\times 800$.

they may then take an oblique course to re-enter the same or another vein and subsequently they may emerge once again on the same or the opposite side. Sometimes they meet or cross other fibres running between two veins (Pl. 49, fig. 4; text-fig. 1E). Marginal fibres could not be seen clearly at any point.

Amplitude of sinuities of cell walls in upper epidermal cells varies from 3 to 14 μ and the lateral distance between two antinodes from 5 to 12 μ . Cells between veins are rectangular and 62–128 μ long and 26–48 μ wide. The thickness of their lateral walls varies, these being generally thicker over and near midrib. The cell walls are 4–7 μ thick in areas between veins and 6–11 μ near and over midrib.

Cells between two veins in the lower epidermis are 48–112 μ long and 40–80 μ wide. Surface of cells is clearly mottled and shows well-marked lighter oval or rounded areas, like those of *R. harkinii*. Surface striations are generally present in the cells over and near the midrib. These run parallel to the longitudinal axis of cells but never radiate from their centre. The guard cells are 37–63 μ long and 15–26 μ wide and the stomatal opening is 4–7 μ . The stomata are generally exposed and not protected by subsidiary cells as in *R. danaeoides*, or their papillae as in *R. harkinii*. The guard cells show clear lignified lateral and polar lamellae of gymnosperm type, which are dissolved after maceration with concentrated nitric acid and potassium chlorate, followed by ammonia.

The side veins and midrib in various leaf fragments show tracheids in abundance. Some of them showing clear spiral (Pl. 49, fig. 6; text-fig. 2D) and annular (Pl. 49, fig. 2; text-fig. 2E) thickenings, but most of them being scalariform (Pl. 49, fig. 5; text-fig. 2B). Some tracheids of the midrib also show alternate biseriate pits (Pl. 49, fig. 5; text-fig. 2C). The fibrovascular elements of midrib and veins sometimes show rounded or oval pinhole-like pits as in *R. danaeoides*.

Comparison and discussion. *Rhabdotaenia fibrosa* agrees with *Macrotaeniopteris feddeni* Feistmantel in shape, size, midrib characters, and above all in having about the same concentration of veins per centimetre. Therefore, perhaps it would have simplified matters if the present leaves were also included under the old species *M. feddeni*, but epidermal structure of that species is unknown. Six specimens of *M. feddeni* in the Museum of the Geological Survey of India, Calcutta (Nos. 5200, 5203, 5204, 5205, 5206, and 5498, figured by Feistmantel 1881, pl. xxi A, fig. 3; pl. xxii A, figs. 1–4; and 1886, pl. 1 A, fig. 1 respectively), were examined to see if they could yield any epidermal and cuticular preparations, but none of them shows any carbon. All are fragments of the middle regions of leaves impressed on ferruginous stone and even in specimens where veins are otherwise clear, no thinner lines representing impressions of interstitial fibres are seen (cf. *Glossopteris fibrosa* Pant, 1958). Accordingly, for the present we presume that our specimens of *R. fibrosa* are distinct from *M. feddeni*. In fact we consider it possible that two specimens (Nos. 5200 and 5498) of taeniopterid leaves, which Feistmantel assigned to *M. feddeni*, may not belong to it because they are bigger than others and show clear impressions of side veins running at an acute angle to the midrib (cf. *Palaeovittaria*), instead of running at right angles to it as is typical of *Rhabdotaenia*.

Among comparable Lower Gondwana forms whose epidermal structure is known, *Rhabdotaenia fibrosa* differs from other species of the genus in having characteristic interstitial fibres. In addition, *R. fibrosa* differs from *R. danaeoides* in having an acute apex (the apex in *R. danaeoides* is obtusely pointed). It differs from both *R. danaeoides*

and *R. harkinii* in having a higher concentration of veins per centimetre (*R. fibrosa* has 15–27 veins per cm. near midrib and 19–31 veins towards margin; *R. harkinii* has 15–18 veins per cm. near midrib and 24–28 veins near margin and *R. danaeoides* has 7–16 veins per cm. near midrib and 8–20 veins towards margin). In *R. harkinii* about half of the total number of veins are forked, but in *R. fibrosa* only one-fifth are forked as in *R. danaeoides*. The epidermal structure of the three species is also quite distinct. The upper epidermal cells in *R. fibrosa* are rectangular and arranged in rows parallel to the lateral veins. Their anticlinal walls are sinuous and generally unevenly thickened, their thickness is generally 4–7 μ in areas between veins over the lamina and 6–11 μ in the region of the midrib. The upper epidermal cells in *R. danaeoides* and *R. harkinii* are polygonal and irregularly arranged. Their sides are straight. The surface of upper epidermal cells in *R. danaeoides* sometimes shows obscure marks of hollow papillae, but these have not been seen in *R. fibrosa* (or even in *R. harkinii*). The sides of lower epidermal cells in all the three species are sinuous, but the walls in *R. fibrosa* and *R. danaeoides* show many more smaller undulations, while the waves in walls of lower epidermal cells in *R. harkinii* are fewer and larger. The figures depicting the amplitude of sinuosities and the lateral distance between two antinodes in the lower epidermis of the three species are:

| Name of species | Amplitude of sinuosities | | Lateral distance between two antinodes | |
|----------------------|--------------------------|----------|--|----------|
| | Range | Average | Range | Average |
| <i>R. fibrosa</i> | 3–13 μ | 7 μ | 11–21 μ | 15 μ |
| <i>R. danaeoides</i> | 5–16 μ | 11 μ | 8–24 μ | 13 μ |
| <i>R. harkinii</i> | 13–28 μ | 19 μ | 20–43 μ | 31 μ |

Surface striations are present almost in every cell of the lower epidermis in *R. harkinii*. In *R. fibrosa* and *R. danaeoides* these are present usually in the lower epidermal cells of the midrib region. In *R. harkinii* the surface papillae are very prominent and generally present in most cells of the lower epidermis, but in *R. fibrosa* and *R. danaeoides* they occur only occasionally in the cells of the lower epidermis of the lamina. The guard cells of stomata in *R. fibrosa* are always exposed and never protected by papillae of surrounding cells as in some stomata of *R. harkinii*. The tracheids in the side veins of *R. fibrosa* show annular and spiral thickenings besides scalariform elements like those described by Pant (1958) in *R. danaeoides* and *R. harkinii*. Some tracheids of the midrib in *R. fibrosa* also show alternate biseriate pits.

R. fibrosa may also be compared with *Glossopteris fibrosa* Pant on account of the occurrence of interstitial fibres. However, it clearly differs from *G. fibrosa* in having side

EXPLANATION OF PLATE 49

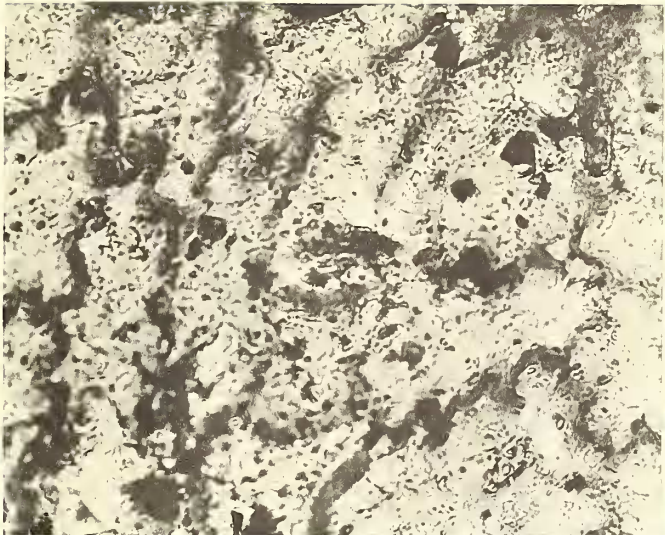
Figs. 1–7. *Rhabdotaenia fibrosa* sp. nov. 1, Apex of a leaf. 233; $\times 1$. 2, Xylem element from a lateral vein showing annular thickenings. 234; $\times 552$. 3, Lower epidermis showing an enlarged stoma with polar and lateral lignin lamellae and epidermal cells with sinuous anticlinal walls. 232a; $\times 447$. 4, A portion of lamina showing lateral veins running parallel to each other (thicker lines) and a few interstitial fibres (thinner lines) between them. 232; $\times 15$. 5, Xylem elements from midrib showing alternate biseriate pits on the lower, left side and also scalariform thickenings elsewhere. 231a; $\times 552$. 6, Xylem elements from midrib showing spiral thickenings. 231a; $\times 1220$. 7, Fragment of middle region of a leaf. 229, $\times 1$.



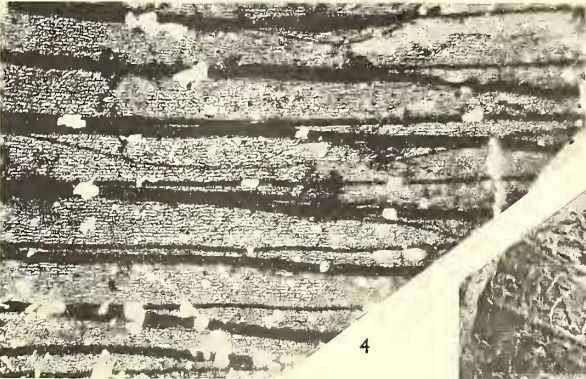
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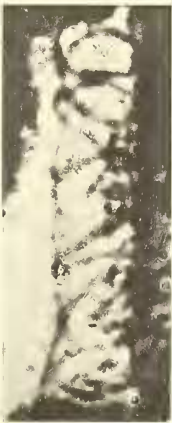
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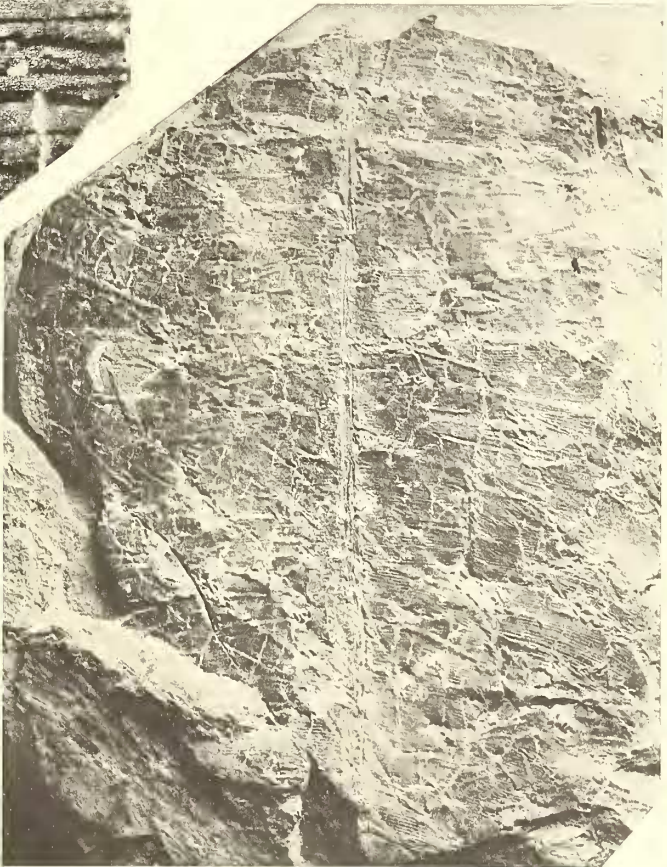
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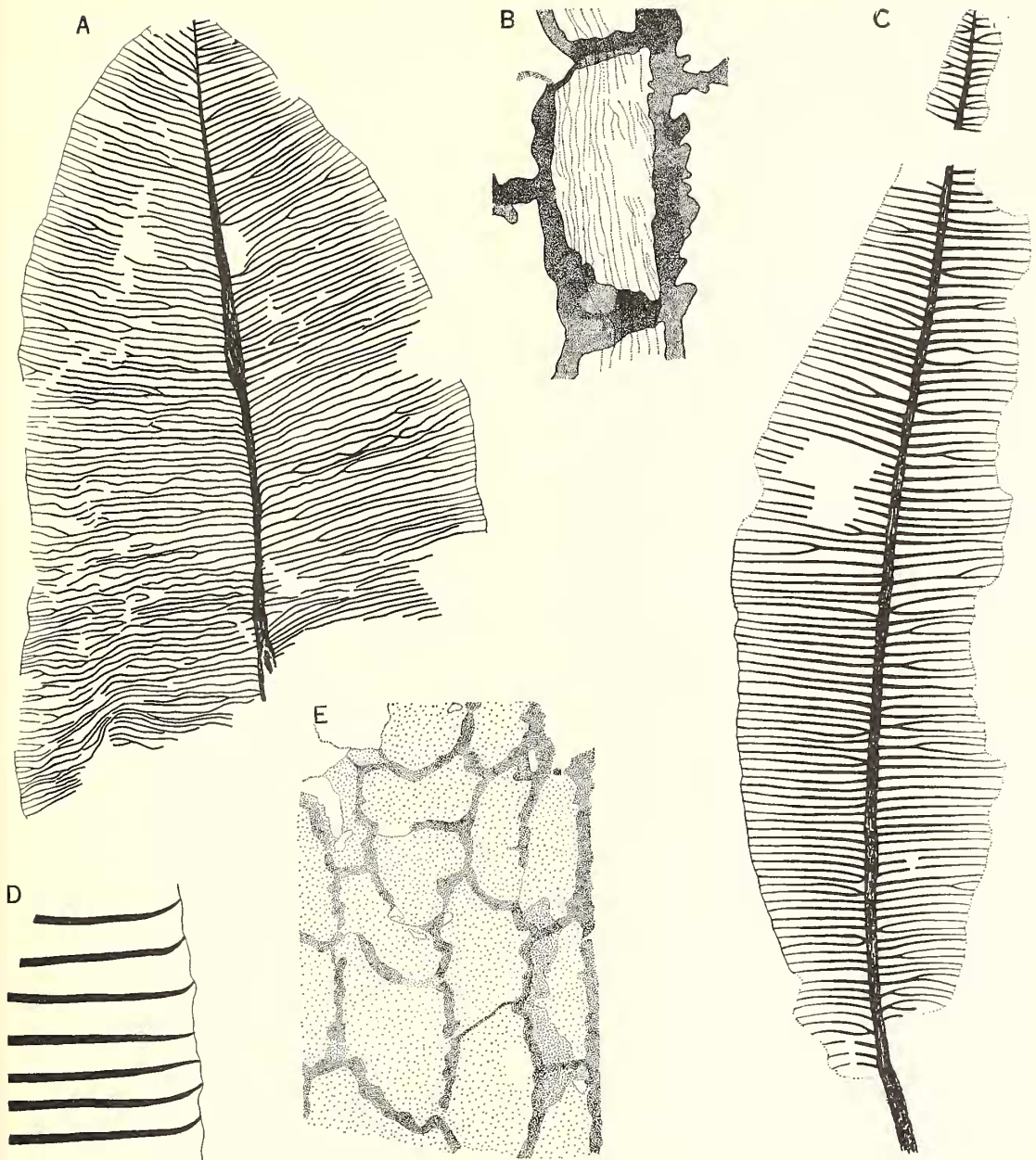
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TEXT-FIG. 3. *Rhabdotaenia danaeoides*. A, Apical portion of leaf showing arrangement of veins (see also Pl. 50, fig. 1). 240; $\times 4/3$. B, An epidermal cell of midrib showing surface striations. 241e; $\times 533$. C, Middle and basal portions of a leaf showing venation. 245; $\times 4/3$. D, Margin of leaf with veins slightly curved towards the apex. 248d; $\times c. 5$. E, A few cells between the veins in text-fig. 5E, more magnified. 238p; $\times 267$.

veins running at right angles to the midrib and in the absence of anastomoses between them. Moreover, the epidermal structure of the two forms is quite distinct.

Rhabdotaenia danaeoides (Royle) Pant

Plate 50, figs. 1–2; text-figs. 2A, 3–6

Synonymy. See Pant (1958).

Emended diagnosis. Leaves oval, oblong, petiolate, 3–9·4 cm. wide and up to 15·9 cm. long, widest in middle region, apex obtusely pointed, base more or less abruptly contracted, margins entire, sometimes slightly undulate. Midrib up to 6·5 mm. wide below, narrower towards apex, showing numerous longitudinal strands in basal part, fewer above. Lateral veins parallel, arising at an acute angle from midrib and almost immediately arching outwards and running at about 90° to midrib, vein ends near margin often slightly curved towards apex. At an average about one-fifth of lateral veins forked once, forking either at points of origin from midrib or elsewhere in lamina, but mostly in middle region; twice forked veins very rare; other veins remain unforked. Cross connexions between veins present but extremely rare. Concentration of veins 7–16 per cm. near midrib (near points of origin) and 8–20 per cm. towards margin.

Upper epidermis of lamina without stomata. Cells between veins straight-walled, polygonal, sometimes showing obscure marks of papillae. Marginal epidermal cells longitudinally elongated, almost straight-walled, leaf substance at margin showing elongated thick-walled cells.

Lower epidermis of lamina stomatiferous. Cells between veins irregularly shaped, 64·0–132·8 μ (93·3 μ) long and 35·2–92·8 μ (60·8 μ) wide, walls sinuous sometimes showing rounded marks of median hollow papillae, becoming gradually straight near midrib. Cells over veins narrower, elongated in direction of veins, walls almost straight. Stomata usually confined to areas between veins, rarely over veins, somewhat unevenly distributed, frequency about 66 stomata per sq. mm., orientation irregular. Stomata haplocheilic. Guard cells 16–28 μ wide and 32–64 μ long, stomatal opening 1·6–8 μ wide. Stomata exposed or more or less covered by subsidiary cells but never overarched by subsidiary cell papillae. Subsidiary cells 3–5, irregular, not forming a ring, polar subsidiary cells like laterals, size and shape of subsidiary cells similar to ordinary epidermal cells.

Upper and lower epidermis of midrib showing straight-walled cells above veins and slightly sinuous-walled cells between them, cells tending to be arranged in longitudinal rows. Cells of lower epidermis showing fine longitudinal surface striations.

Upper cuticle of lamina showing cells with somewhat obscure outlines, cell walls thin. Lower cuticle of lamina stomatiferous like lower epidermis. Cells between veins with

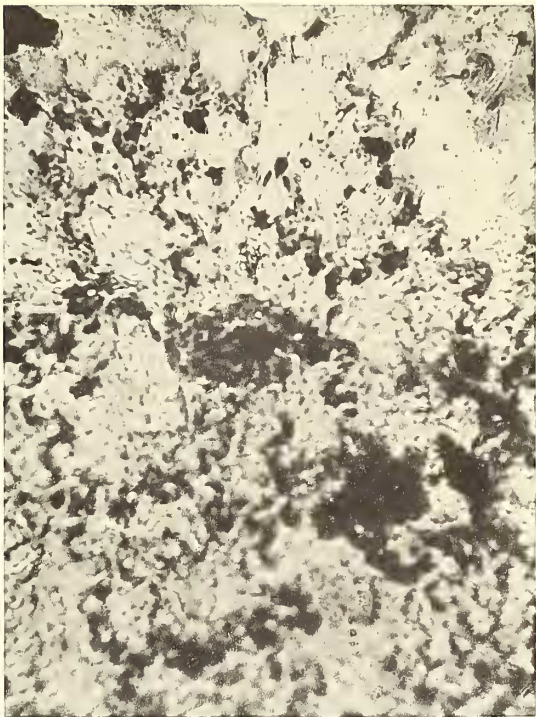
EXPLANATION OF PLATE 50

Figs. 1, 2. *Rhabdotaenia danaeoides*. 1, Apical and middle portion of a leaf showing venation. The lighter patches are caused by the removal of carbon in pulls. 240; $\times 1$. 2, Lower epidermis showing an exposed stoma. 245b; $\times 471$.

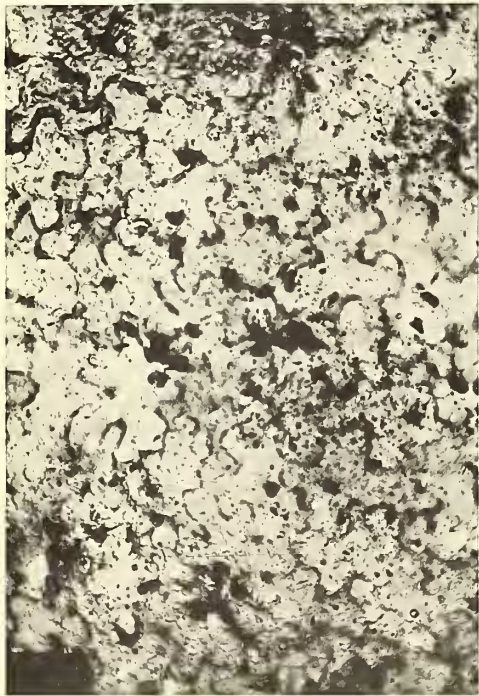
Figs. 3, 4. *Rhabdotaenia harkinii*; V34454. 3, Lower epidermis showing sinuous-walled cells and irregularly placed protected stomata, $\times 193$. 4, Lower epidermis with papillate epidermal cells and an exposed stoma, $\times 400$.



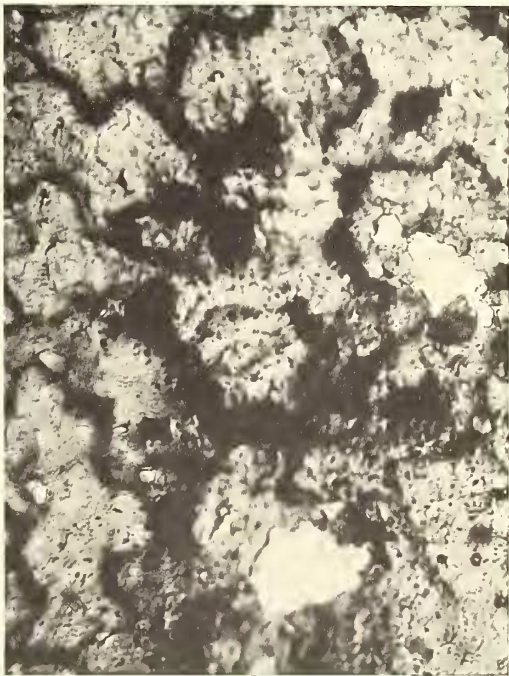
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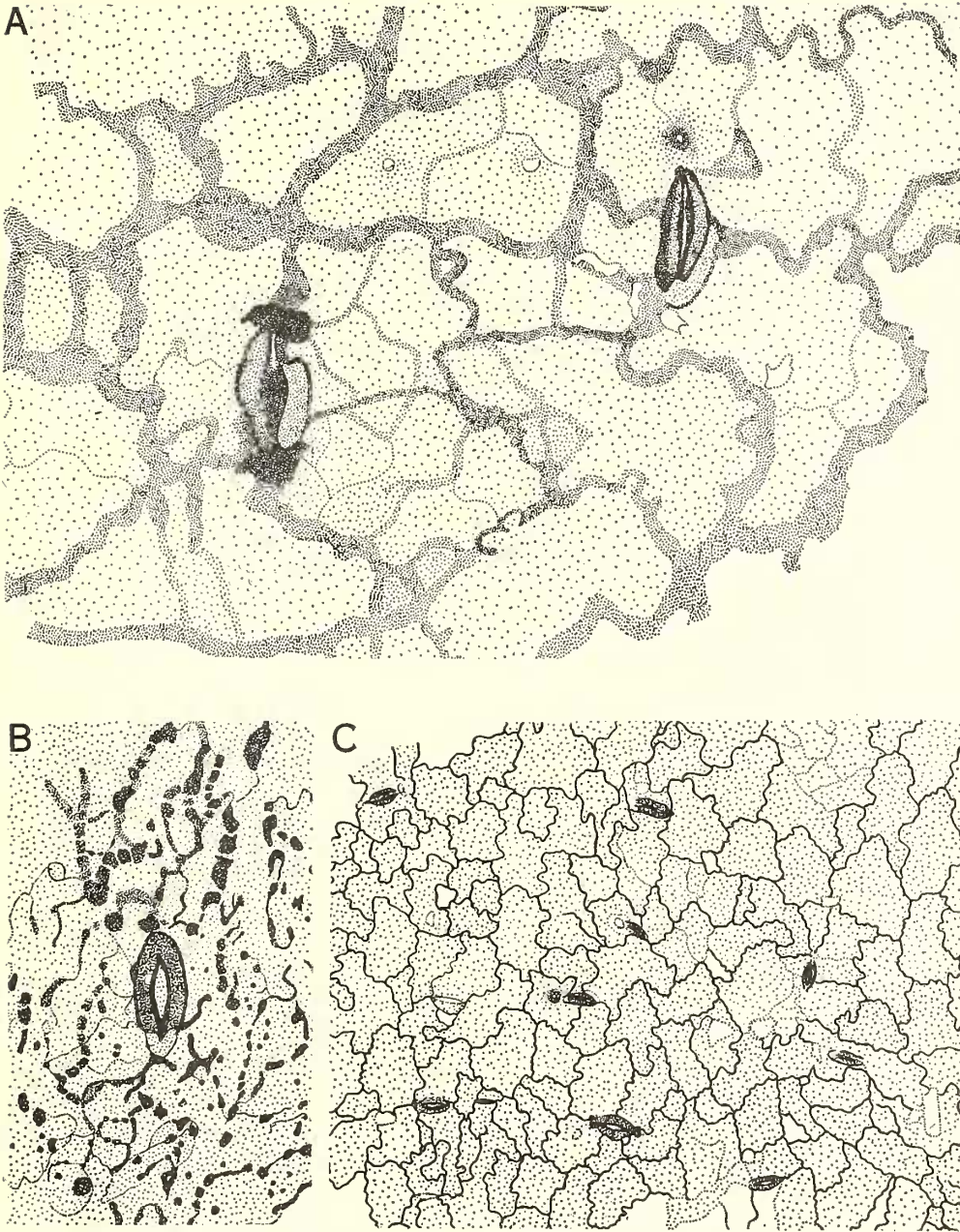
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TEXT-FIG. 4. *Rhabdotaenia danaeoides*. A, Lower epidermis with two stomata, one (left) showing lignified polar lamellae on the two poles and the other (right) showing a hollow mark of papilla in one of its subsidiary cells. 238a; $\times 400$. B, Lower cuticle showing a stoma and obscure sinuous-walled cells (under phase-contrast microscope). 308n; $\times 301$. C, Lower epidermis showing sinuous-walled cells. The stomata are irregularly placed in between the veins. 238a; $\times 125$.

obscure cell walls usually appearing broken, but sometimes showing sinuous waves; cell walls below veins less obscure, straight.

Neotype. Brit. Mus. (N.H.) Palaeont. Dept. No. V4191. Figured Royle (1833, pl. 2, fig. 9) and Arber (1905, pl. 5, fig. 1).

Isotypes. Specimen Nos. 237–330 deposited in the Divya Darshan Pant Collection, at present located in Botany Department, University of Allahabad.

Locality and horizon. Raniganj coalfield, India, Lower Gondwana.

Description. The emended diagnosis is based on ninety-five leaf fragments from the Raniganj coalfield, India (including five apices, one base, and eighty-nine pieces from the middle region of leaf laminae). Some of the leaves appear to have been quite narrow, about 3 cm., but others were up to 9.4 cm. wide. The midrib was up to 6.5 mm. wide in the basal part. Lateral veins, which run almost straight up to the margin, are sometimes slightly curved upwards towards the apical region (text-fig. 3D). In places the veins appear sinuous (Pl. 50, fig. 1; text-figs. 2A, 3A), but, as already pointed out by Pant (1958), such sinuosities are obviously due to a displacement of the veins inside the epidermal and cuticular coat of the leaf, when its more delicate mesophyll tissue has partially or wholly dissolved.

The margins of simple spatulate leaves are seldom torn. In the absence of regular anastomoses between the side veins, like those found in *Glossopteris* and *Gangamopteris*, it was difficult to understand how such large laminae remained intact, but a specimen with a well-preserved margin reveals that this was possibly due to the presence of longitudinal strands of thick-walled cells running parallel to the margin (text-fig. 6B, C). The thick-walled marginal cells appear to be fibrous, but at one point (text-fig. 6C) their walls show pits like those of xylem, suggesting that there could even be some marginal tracheids present among them.

The number of bifurcated veins is usually higher in the middle region. The concentration of veins per cm. is higher in the apical and basal portions (at the point of their origin from the midrib). In different leaf fragments the ratio of once-forked lateral veins and those remaining unforked ranges from one-third to one-fifteenth.

The typical sinuous-walled cells of the lower epidermis are clearly seen in most of the specimens, but fragments of the upper epidermis are seen only in one specimen. The cells of upper epidermis seem to be relatively less sinuous-walled or with almost straight walls like the cells over the meshes of the veins in the midrib (text-fig. 3E).

The lateral veins and midrib show abundant tracheids. Some of them have spiral (text-fig. 6F) and reticulate thickenings (text-fig. 6E), but most of them are scalariform (text-fig. 6A). Along with the typical xylem cells of the veins and the midrib are seen some thick-walled elongated elements with oval or rounded pinhole-like pits. They may represent fibres or tracheids (text-fig. 6D, and also Pant 1958).

Comparison and discussion. Pant (1958) has already discussed the differences between *Rhabdotaenia* and other leaves of *Taeniopteris* type which possess haplocheilic stomata, such as *Doratophyllum* (Harris 1932) and *Bjuvea* (Florin 1933). The Jurassic leaves of *Nipaniophyllum raoi* (Sahni 1948) also have haplocheilic stomata. Like *Rhabdotaenia*, their midribs contain a number of parallel veins. However, they belong to a different age and their size, form, and epidermal structure are clearly different. Moreover, they occur